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Ecology of epigeic Collembola in the Netherlands

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0. Introduction

It is paradoxical that ecological studies (and the systematics) of epigeic Collembola lag considerably behind those of edaphic species. Only a few papers deal extensively with this fauna. Notable exceptions are reported by Gisin (1948), on the epigeic Collembola of the Alps, by Stach (1959), on the Collembola of the Tatra national park, and by Cassagnau (1964), on the epigeic Symphypleona of the Pyrenees. Since the ecological responses of the various species seem to vary appreciably in different parts of their ranges, I present a brief survey of the Dutch epigeic Collembolan fauna.

Two drawbacks that strongly influence the work on this subject must be mentioned at the outset. Many species are dispersed in a highly irregular way. This patchiness, together with the inevitably rough collecting method, in a discontinuous habitat means that numbers captured vary to a large extent within a few meters. Moreover, the effectiveness of a sweeping net is so dependant on the structure of the vegetation that I could not use Gisin's scale of abundance which is based on the exact number captured. Instead of this, I work with a subjective scale ranging from incidentally, sparse, untile mass occurrence.

However, as already stated by Cassagnau, the phenomena and habitat preferences are mostly so evident, that a formal numerical approach is hardly warranted. Another statement of Cassagnau that could be verified to a large extent is that usually only one species is clearly dominant. Notable exceptions to this rule occur especially in the fauna of rotting branches, tree boles, etc. Since Gisin, in contrast to Cassagnau, was fairly occupied in his study with this group of species, his species lists do show rather often the occurrence of some codominants.

Although in the following lines I shall discuss mainly species that are doubtless epigeics, I must draw attention to the fact that some species that generally are considered to be hemiedaphic, or even eu-edaphic have passed to a more or less epigeic way of life. Examples of this are in the Netherlands *Protaphorura quadriocellata* and *Neanura muscorum*, that occur regularly (and the first species even exclusively) under rotting branches, together with species as *Dicyrtomina minuta* and *Allacma fusca*. Otherwise, undoubted epigeics as *Tomocerus* species, and even *Entomobrya nivalis* belong to the edaphic or hemi-edaphic fauna in their juvenile stages. With a concept of the epigeic fauna as broad as this, I know presently 50 species in the Dutch fauna. I shall discuss now some of them in more detail.

1. Fauna of various habitats

1.1. Rotting wood

At the borderline of the euedaphon is a number of species that frequent lumps of rotting wood, etc. Most common in this habitat are *Protaphorura quadriocellata* (Gisin, 1947), *Neanura muscorum* (Templeton, 1835), some species of *Tomocerus* and *Lepidocyrtus*, *Orche-cincta* (Linnaeus, 1758) and *villosa* (de Villers, 1789), *Heteromurus nitidus* (Templeton, , some *Sminthurinus* species, *Lipothrix lubbockii* (Tullberg, 1872), *Allacma fusca*)aeus, 1758) and *gallica* (Carl, 1899), *Dicyrtomina minuta* (O. Fabricius, 1783) and *toma fusca* (Lubbock, 1873).

Naturally, all these species occur more or less exclusively in woods, but the ubiquitous *Neanura muscorum*, *Tomocerus minor*, *Lepidocyrtus lignorum* and *Orchesella cincta* can be found under boards and poles far from any wood, provided that the habitat is not too dry.

Protaphorura quadriocellata is a rather common species; together with *Dicyrtomina minuta*, *Lepidocyrtus lignorum* and to a less extent *Dicyrtoma fusca* it forms the winter fauna of rotting branches. It is striking that *Protaphorura armata* (TULLBERG, 1869) which is very common in the edaphon, never occurs in the habitat of its near relative *quadriocellata*.

The species of *Tomocerus* that occur in the Netherlands are *T. minor* (LUBBOCK, 1862), *longicornis* (MÜLLER, 1776), *flavescens* (TULLBERG, 1871) and, but as a rare species, *vulgaris* (TULLBERG, 1871). I cannot find a difference in habitat preference between any of these, except that *minor* is much more ubiquitous. *T. flavescens* is decidedly more common than *longicornis*. GISIN (1948), was also unsuccessfull in finding ecological differences between *longicornis* and *flavescens*, anyway at low altitudes (in higher altitudes *flavescens* was the more hygrophilic).

In the Netherlands the genus *Lepidocyrtus* is represented by *L. curvicollis* BOURLET, 1839, *cyaneus* TULLBERG, 1871, *lanuginosus* (GMELIN, 1788), *lignorum* (O. FABRICIUS, 1781), *ruber* SCHÖTT, 1902, and *violaceus* LUBBOCK, 1873. *L. curvicollis* is restricted to artificial caves, namely the marl quarries in the south of the Netherlands; *ruber* and *violaceus* are rare and seemingly restricted to the hemiedaphon; *cyaneus* is a not very strictly epigeic. *L. lignorum* and *lanugionsus* live mainly on rotting wood, but at present *lanuginosus* is known from only one locality.

In contrast to records from other countries *Heteromurus nitidus* seems to be a rare species in the Netherlands, seemingly restricted to woods on rich damp soil with a quick and complete litter breakdown. As in many other hemi-edaphic and epigeic species the immatures of *Orchesella cincta* live (in vast numbers) in the litter whereas the adults occur in more open situations. *O. cincta* is a rather hygrophilic species and only sometimes after or during a rain period it ventures on tree boles.

Within the genus *Sminthurinus* I shall limit´mention to a short but abundant occurrence of *Sminthurinus flammeolus* in the winter of 1972/73. *Allacma gallica* lives only in the dune area in the Netherlands, whereas *A. fusca* is present in all deciduous woods. Both species are often seen in high numbers on tree boles; they occur only rarely on the herb layer and exclusively in rather damp situations.

GISIN (1948), considers *Dicyrtoma fusca* as a more or less xerophilous species, in contrast to its vicariant *Dicyrtomina minuta*. The situation in the Netherlands is rather different. *D. fusca* occurs in most types of deciduous woods, throughout the year, and I do not know of a preference for a particular humidity value. *Dicyrtomina minuta*, however [inclusive *D. saundersi* (LUBBOCK, 1862) and *D. ornata* (O. FABRICIUS, 1783)] also occurs in all kinds of deciduous woods, but has a marked preference for the winter half year. Especially *minuta* can at times be very abundant.

1.2. Tree boles

The tree trunk is the habitat of *Anurophorus laricis* NICOLET, 1842, *Willowsia nigromaculata* (LUBBOCK, 1873) and *platani* (NICOLET, 1841) and *Entomobrya albocincta* (TEMPLETON, 1835). It seems that, with the possible exception of *albocincta*, these species have become much rarer in the last thirty hears. In the Fauna of the Netherlands, Buitendijk published in 1941 a contribution on the Collembola. Although this was based on relatively restricted material, the number of records given by her of the above mentioned species is high compared with my findings. The dwindling number of old, overgrown trees, and the general decline in epiphytic vegetation may be the explanation for this.

1.3. Houses

Of the species that occur in or associated with houses, I mention a mass occurrence of *Entomobryoides purpurascens* (PACKARD, 1873) in a house at Eindhoven. (GISIN, 1962, discusess three similar cases in Paris and Genève). Another occasional plague in houses is *Bourletiella hortensis*. Twice *Willowsia buski* (Lubbock, 1869) is found as a synanthropic. *Seira domestica* (Nicolet, 1841) is in the Netherlands restricted to houses, where it is found not infrequently, though never in any number.

1.4. Vegetation

1.4.1. Arthropleona

Finally I must discuss the species that haunt the vegetation mat. In the genus *Entomobrya*, I can report the species *E. nivalis* (Linnaeus, 1758), *multifasciata* (Tullberg, 1871), *lanuginosa* (Nicolet, 1841), and *muscorum* (Nicolet, 1841). Moreover, *E. quinquelineata* (Börner, 1901) is recorded from the Netherlands by Buitendijk, but I have not collected this species there myself.

Most interesting is the remarkably strict vicariance between *E. multifasciata* and *nivalis*. The first species is rather common in vegetation that is devoid of trees and shrubs. *E. nivalis*, on the contrary can almost exclusively be found in vegetations with a wood stratum.

Here, as elsewhere in Europe, *nivalis* is a very common species, that can be beaten from deciduous as well as from coniferous trees, often from a considerable height. The pigmentation of the specimens is very constant, and in the epigeic fauna annoying "pallida-forms" are almost absent. As is already remarked by Agrell (1934), in the canopy fauna *E. nivalis* is represented only by adults, and the juvenile stages are almost exclusively restricted to the litter below. The question where, and how, oviposition in this species takes place has still to be tackled.

Entomobrya multifasciata is referred to sometimes in literature as a xerophilous species, and as a matter of fact the species can be found in very dry habitats, e.g. almost vegetationless hot dune valleys. However, the species is just as common in some wet, rough grasslands. Adults are almost exclusively swept with the net whereas juveniles are mostly restricted to the soil strata below.

Entomobrya lanuginosa is not a common species, of which I have but one good series, collected from a cultivated fertilized meadow with an opulent but monotonous grass vegetation. The species was collected in company with *Sminthurus viridis*.

Entomobrya muscorum is collected only in the extreme South of the Netherlands.

Of the species of *Orchesella*, only *O. flavescens* (Bourlet, 1839), belongs to the fauna of the herb layer. It is not a common species, mostly swept from macrophytes in light deciduous woods on not too moist soils. Gisin (1948), discusses a vicariance between *Entomobrya muscorum* and *Orchesella flavescens*, the first species being characteristic for xerophilous woods, the second one for damp woods. The limited number of records from the Netherlands does not permit me to comment on this.

The only species of *Lepidocyrtus* that truly (though not exclusively) belongs to the epigeic auna is *L. cyaneus*, that occurs not infrequently in rather dry grasslands.

1.4.2. Symphypleona

Two of the very common Dutch species in the epigeic fauna are *Sminthurus viridis* (Linnaeus, 1758) and *nigromaculatus* (Tullberg, 1872). These two species show a most perfect vicariance. *Sminthurus viridis* is very common, and occurs often in large numbers, in well cultured grasslands, with a good and rather stable moisture content of the soil, and an opulent vegetation that never wilts. Grazing and mowing is perfectly tolerated, but the species does not occur frequently under a dense tree cover. *Sminthurus nigromaculatus* is as common as *viridis*, equally in grassy vegetations devoid of a wood stratum, but this species needs a more or less natural vegetation, with a variable moisture content, so that the vegetation may completely wilt after spring. Because *viridis* is so dependent on agriculture, and *nigromaculatus* so decidedly avoids this, the border line between two population belonging to the different species may be as sharp and as clear-cut as a fence of barbed wire.

At present I know four species of the genus *Bourletiella* in the Dutch fauna. These are *B. hortensis* (FITCH, 1863), *viridescens* (STACH, 1920) and *arvalis* (FITCH, 1863). Moreover, another species occurs in dense populations in low, dry dune grasslands; since all populations of this species studied are subject to a phenotypical neutralisation of their secondary sexual characters (in particular all males are affected) an identification has to be postponed. This species will be treated in a separate study.

All of these require a low, sparse vegetation. The most common species is *viridescens*. This species frequents, sometimes in extremely large numbers trodden lawns and similar vegetations. Moisture content of soil does not seem to influence sensibly the abundance of *viridescens*. Drought, however, is decidedly better tolerated by this species than by *Sminthurus viridis*. *S. nigromaculatus* and *B. viridescens* are often found together, even as codominants. When, however, the grass vegetation becomes too high and rough, *viridescens* looses ground in favour of *nigromaculatus*. A similar picture of the ecological requirements of *viridescens* is evident from the papers of GISIN and CASSAGNAU. *Bourletiella hortensis* seemingly prefers an even more open sparse vegetation than *viridescens*, but *hortensis* needs a rather moist soil, anyway periodically. GISIN mentions this species among those typical of steppe-like grasslands, but in the same paper gives a description of what in the Netherlands is a normal situation: a large colony at the gravely bank of Lac Léman, in a site that is submerged annually. The species is rather often found in synanthropic situations (probably in connection with its preference for almost bare habitats): on pavements, gravel roads, sports fields, flat roofs covered with gravel, etc. From the last habitat they are often driven by drought down into the houses, where they may suddenly appear in vast and most annoying numbers. Each year some of these cases are brought to my attention.

Of *Bourletiella arvalis* I know but one colony, in an open, low, damp trodden and slightly polluted grass vegetation.

Four species of *Heterosminthurus* do occur in the Netherlands, namely *claviger* (GISIN, 1958), *bilineatus* (BOURLET, 1842), *insignis* (REUTER, 1876) and *novemlineatus* (TULLBERG, 1871).

Heterosminthurus claviger is in the Netherlands invariably found in dry habitats, sometimes in dry heather on poor pleistocene sand, sometimes in rather high, withered grass vegetations (with *Bourletiella viridescens* as accompanying species, and *Sminthurus nigromaculatus* as codominant). The species is described from wet alpine meadows, and was according to the list of localities, often swept from dwarf shrubs; on the contrary, I myself found the species in the Alps in sunny meadows on a south slope, with a low vegetation. MURPHY (1960), described the synonymous *Bourletiella craggi* from Calluneta and moorland in England, and I know a locality in Germany, just across the Dutch frontier, where *claviger* abounds in the heather on a peat moor. Evidently, although all Dutch localities are on a very dry substrate, the species can be expected in wet habitats as well. A general preference for heather vegetations — and some of the grass habitats are in reality dominated by *Deschampsia flexuosa* (L.), which occurs often on degraded heather — is evident. *Heterosminthurus bilineatus*, in contrast is limited to rather moist vegetations. They must not be covered by a wood stratum, but otherwise the vegetation may be as low as a mat of *Hydrocotyle*, or as high as the unmowed meadow vegetation of a ditch border. *Heterosminthurus novemlineatus* is only found on marsh vegetations, at the border of small, more or less oligotrophic inland waters, on the pleistocene. This type of water is quickly disppearing, due to pollution, recreation and urbanization.

Heterosminthurus insignis is more widespread, and can be found on low, moist vegetations (both on holocene and on pleistocene), often together with *Heterosminthurus bilineatus* and sometimes *Bourletiella viridescens*. A similar habitat (border vegetation of mountain streams, with *Carex* and *Juncus*), is described by GISIN and CASSAGNAU. The last complex that must be discussed are the five Dutch species of the genus *Deuterosminthurus*: *D. sulphureus* (KOCH, 1840), *repandus* (ÅGREN, 1903), *pallipes* (BOURLET, 1843), *bicinctus* (KOCH, 1840), and *flavus* (GISIN, 1946).

Most common by far is *D. repandus*. This species can be encountered in a variety of landscapes. Soil humidity does not much influence the abundance of this species, which I know from many localities in marshy regions, but just as well from very dry dune areas. A light shadow does not influence this species, but *repandus* is not present in denser woods. Essential for this species is a rather high macrophyte vegetation, for instance thistles, nettles, *Eupatorium*, *Pulicaria*, *Salix repens* etc. Such vegetations are often present in the border strips of paths and roads. In the central Pyrenees, *D. repandus* is not present, and its place seems to be taken by *D. beckeri* (COINEAU et DELAMARE, 1961). GISIN (1948) reports *repandus* (as *Bourletiella mixta* GISIN, 1946) from all types of grass vegetations. Since his grass vegetations only seldom seem to be identical with the monotonous low meadows of the Netherlands, with their poor species composition, this statement of his does not necessarily contradict my results.

Deuterosminthurus pallipes, distinguishable from *repandus* only by its pigmentation, lives in quite another habitat, namely on dwarf shrubs (*Vaccinium*) in fairly dry, light deciduous woods, more seldom on *Erica* and *Calluna* in the open. In this habitat *repandus* occurs only rarely. GISIN (1948) mentions *pallipes* as inhabitant of steppe-like grasslands.

Deuterosminthurus sulphureus occurs, often in astonishing numbers in high, coarse grass vegetation, usually on rather damp soil; often the habitat has a strong ruderal aspect, as is also evident by the abundance of many nitrophilous herbs (thistles, *Tussilago*, *Epilobium hirsutum*). GISIN (1948) argues, that *sulphureus* is much less adapted to withstand drought and heath than *repandus*. Consequently, there is in the neighbourhood of Genève a gradual replacement of *sulphureus* by *repandus* as summer proceeds. He gives a lively description of this procedure, but in the more temperate climate of the Netherlands an extinction as complete as in Switserland of *sulphureus* is probably only seldom attained. In the first weeks of August of this year I still saw very populous colonies of *sulphureus*.

In fresh meadows in South Central France, *sulphureus* forms together with *Sminthurus viridis* and *Heterosminthurus bicinctus* a very frequent combination, as is noted by CASSAGNAU (1964).

Deuterosminthurus flavus and *bicinctus* are morphologically just as similar as *repandus* and *pallipes*. Yet the vicariance between the last two species is of such nature that this would be an argument in favour of their being separate species; moreover, BRETFELD (1971), reports some differences in premating behaviour. The situation in *flavus* and *bicinctus* is quite opposite. BRETFELD reports mixed premating couples. Moreover, anyway in the Netherlands the ecology of both species is so alike, that they are mostly found together. The species have a strong preference for macrophyte vegetations (just as the other species of the genus) but they moreover need a high air humidity. They are mostly found under a tree cover, in damp woods in the neighbourhood of marshes, lakes etc., but I know also a locality where the species both occurred on the border vegetation of a canal, without a tree cover. The situation in other regions, however, is evidently not so simple. CASSAGNAU found only *flavus* in the Central Pyrenees, where the species occurs on macrophytes above the altitude where *Sminthurus viridis* could survive. GISIN (1948) even described a neat vicariance between both species, since *flavus* seems to occur in his region of investigation in xerophilous woods, *flavus* and *bicinctus* together occur in damper woods, whereas in very dark and shadowed macrophyte vegetations *bicinctus* is present without *flavus*.

2. Conclusion

In conclusion I think it justified to regard vegetation structure as the prime factor in the habitat of epigeic Collembola. Soil moisture may play a role in the egg and immature stages. Doubtless a fruitful extension of the research would be a systematical assessment of the degree to which the soil moisture present is indeed accessible. VANNIER, in a number of publications, has drawn the attention of Collembola ecologists to this key concept, which may explain apparent contradictions as for instance the occurrence of *Heterosminthurus claviger* in dry wilted dune vegetation and in peat moor heather.

3. Literature

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